beyond what was laid down by the rivers in time of flood to maintain their grade across the sinking basins was carried through to the shallow sea which lay on the surface of the continent to the southwest. The relations were somewhat similar to those which now prevail between the ranges of the North American Cordillera and the Tertiary basins which lay between them and especially on the west between the Sierra Cascade chains and the Coast Ranges. The Great Valley of California may therefore in the present epoch, both in physiography and in climate be cited as a striking illustration of the nature of the Old Red Sandstone basins.

[1] Macnair and Reid, *Geol. Mag. Decade* IV, 3, 106–116, 217–221 (1896).

[2] Goodchild, J. G., The Older Deutozoic Rocks of North Britain, *Geol. Mag. Decade* V, 1, 591–602 (1904).

[3] Walther, J., *Geschichte der Erde und des Lebens*, 259 (1908).

[4] Barrell, J., Relative Geological Importance of Continental, Littoral, and Marine Sedimentation, *J. Geol.*, **14**, 316–356, 430–457, 524–568 (1906); Relations Between Climate and Terrestrial Deposits, *Ibid.*, **16**, 159–190, 255–295, 363–384 (1908).

[5] Barrell, J., The Upper Devonian Delta of the Appalachian Geosyncline, *Amer. J. Sci.*, **36**, 429–472 (1913), **37**, 87–109, 225–253 (1914).

[6] This paper was given in brief form at the meeting of the American Society of Vertebrate Paleontology at New Haven, Conn., on December 26, 1907 [Loomis, F. B., Report of the Secretary, The American Society of Vertebrate Paleontology, *Science*, **27**, 254 (1908)], and more fully at the meeting of the Geological Society of America at Washington, December 28, 1915. It will be published in full in the *Bulletin of the Geological Society of America* in 1916. The present paper is a digest and its chief importance is because of its bearing on the environment of early vertebrates. In that way it is introductory to a paper on the Influence of Silurian-Devonian Climates on the Rise of Air-breathing Vertebrates which will follow in these PROCEEDINGS.

[7] Pirsson-Schuchert, *Text Book of Geology*, Part II, *Historical Geology*, by C. Schuchert, 714–721 (1915).

THE INFLUENCE OF SILURIAN-DEVONIAN CLIMATES ON THE RISE OF AIR-BREATHING VERTEBRATES

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Received by the Academy, July 17, 1916

The problems of organic evolution have many aspects and ramify into many fields of science. The subject was at first embraced chiefly in the domain of the old time naturalist—zoologist or botanist. But the problems of variation and heredity have passed into the hands of the experimental evolutionist; and there are other problems whose answers are found in the geologic record—but these are of two rather opposite aspects. On the one hand, the paleontologist specializes particularly on the organic features, the successions and relations of fossil faunas or floras. On the other hand, it is the work of physical and historical geology to restore the ancient environments. The relations of the environments to the biotas is a field wherein physical geology and paleontology meet, to give a better understanding of the underlying physical surroundings associated with organic response and progress. It is from the standpoint of physical and historical geology, rather than from that of paleontology that the present study is made.

In this subject are two major problems—first as to the environment in which fishes developed; second, the changes in the environment and the associated organic responses which brought forth amphibians from fishes. It is the solution of the second problem which is here especially sought,[1] but it involves a statement of the evidence in regard to the first.

The question in regard to the origin of fishes is as to whether they developed first in the sea and later invaded the land waters, as has been generally assumed, or whether their expansion was in the opposite direction—from rivers to embayed waters and thence finally to the sea. Chamberlin appears to have been the first to have seriously suggested that the latter may have been the real direction of their emigration.[2] He pointed out that the fishes appeared as fossils only in the embayed waters until they had attained such dominance that they spread into the truly oceanic realm. Their body form, furthermore, Chamberlin notes, is peculiarly adapted to the stemming of currents and suggests an initial adaptation to rivers.

The evidence for this hypothesis of the continental origin of fishes has been examined by the writer, by taking up the earliest faunas and studying the mode of origin of the associated sediments. The results strongly support Chamberlin's position. The exclusively marine habitats of the lowest remaining chordates, constitute really negative evidence on the subject, for these forms are far removed from fishes, and they leave no fossil record. The original habitats may have been far wider and the progressive forms may have lived a freer life than is shown by these retrogressive and more or less aberrant relics. The positive evidence given by the early fish fossils is more definite and conclusive. A review of this is as follows:

The earliest known ostracoderm remains were found by Walcott in 1891 near Canyon City, Colorado, in a horizon belonging to the base of the Middle Ordovician, in sandstones *which rest upon the Pre-Cambrian.*[3] These sandstones are marginal marine deposits, holding species of Lingula, Orthoceras, and Beyrichia. With these are found abundantly at several levels waterworn scales and plates of ostracoderm fishes. The sandstones are succeeded by marine limestones of Trenton age, but in the limestones, although marine fossils are abundant, the fish remains are absent. If we seek to interpret the origin of these sandstones and their fish remains, it is to be noted that the thickness, 86 feet, is large to have been formed by wave action on a nearly base leveled land. But rivers bring most of the sediment to the sea which is laid down as sandstone, and it is probable that most of this sand was of river derivation. The waterworn character of the fish remains indicates a degree of transportation which the other fossils do not show, and suggests driftage into the region of burial. The absence of all fish remains in both Ordovician and Silurian deposits of solely marine nature strengthens the view that these rare and fragmentary finds were floated into the marginal waters from the rivers.

In mid Silurian red shales of Pennsylvania and in the Upper Silurian Ludlow rocks of Great Britain have been found the next clear appearance of fish remains, mostly of ostracoderms, in associations which seem to indicate at this geologic stage a life of these bottom dwellers not exclusively in the rivers but also probably in protected and brackish embayments of the sea. More clearly, however, they did not yet live in the open sea.

The first true fish fauna, as represented by sharks, in better preservation and considerable variety, is found in the Lower Old Red Sandstones of the Caledonian basin. These are lowest Devonian in age. But the sediments are of a different nature from the marine or brackish water deposits of the Ordovician and Silurian which held the earlier fossils. Viewed in the light of the modern knowledge of the nature of alluvial deposits, the sediments of the Old Red Sandstone are interpreted as having accumulated as river deposits on flood plains or in shallow lakes of an interior basin, lakes subject to marked shrinkage in area during the dry season.

The ganoid fishes appear for the first time and in force in the Middle Old Red Sandstone formations of the Orcadian basin of northeastern Scotland, twenty species belonging to seven genera being known from that basin. Dipnoans also appear at the same time. The enveloping deposits are regarded as Lower Devonian in age, though younger than the deposits of the Caledonian basin.

In contrast to this land water record of the lowest Devonian, the sharks are not found in declaredly marine rocks until at least the Middle

Devonian, and they did not dominate the sea in such exclusive fashion as they dominated the continental deposits of the Lower Devonian until the opening of the Mississippian (Lower Carboniferous) period. In contrast also to the abundant ganoid fauna in the continental waters, only a single species of ganoid is found in the marine Ulsterian (Middle Devonian) rocks of the interior of North America, and they have but scanty representation in the seas until the Mesozoic era. This record appears to show conclusively that the center of piscine evolution was within the land waters, and that the ganoids represented a closer adjustment to that environment than did the sharks.

This brings us to the second problem, the relation of environment to the origin of the amphibians. The nature of the sediments shows that through Silurian and Devonian times the climates, although subject to variation, tended to be warm and semi-arid, that is, marked by a pronounced alternation of wet and dry seasons. In the middle Silurian in fact a high degree of aridity existed in certain regions. The initial development of ganoids, distinguished in their organization from sharks by their capacity to supplement the use of water in respiration by the direct use of air in an air bladder, probably goes back to this Silurian epoch of aridity; since in the Middle Old Red Sandstone stage they are already well differentiated and expand in numerous species through the fresh waters. We must look to the previous period therefore for their origin. During the Upper Devonian the climate became more markedly semi-arid than in the Lower Devonian. Then the traces of sharks disappear completely from the fresh waters, but dipnoans and ganoids continue to exist. This migration of the sharks in habitat is logically to be correlated with the fact that elasmobranchs have no air bladder, not even in rudimentary or vestigial form, whereas the other two orders are so provided. It is notable that the few living species of dipnoans, or lung fishes, are restricted at the present time to tropical regions whose flowing waters are restricted to a wet season, and show such marked adaptations for surviving through seasons of drought that in those environments they possess a permanent advantage over other fishes.

The fossils of fishes in the Old Red Sandstone are apt to be crowde d into occasional layers and are associated with bitumen, indicatingin those layers an unusual amount of organic matter buried without being exposed to atmospheric oxygen. Judged by the environment, they appear to have died in shoals owing to crowding into the foul waters of pools shrinking in the dry seasons. The seasons of drought formed the critical factor in their environment. No traces of amphibians are found, though by the law of anticipation they must have been in existence in Upper Old Red Sandstone times; since they are typically developed at the opening of the following period. The amphibians seem therefore to have originated in more limited regions where fishes could not survive and the waters were not sufficiently permanent for the preservation of their remains.

The preceding arguments have been drawn from the geologic record. Let us now turn to another record,—that embalmed in the nature of living vertebrates, especially lung fishes and amphibians; for they preserve practically unaltered a stage of respiratory and circulatory evolution which had been attained in the Devonian. We may find by examining their organic nature whether the development of lungs was a spontaneous, internally directed organic advance, giving increased activity and efficiency, or whether at first it was a mere makeshift response to the pressure of adverse external conditions.

The air-bladder of ganoids and higher fishes is related to the intestinal region, not the pharyngeal region, as is shown both by its direct connection with the oesophagus in ganoids and in the embryos of other fishes. The blood system shows the same, the dipnoans, ganoids and amphibians having the air-bladder or lungs supplied with blood from a *branch of the fourth efferent gill artery.* In each round of the circulation only a portion of the blood is passed through the primitive lungs. The efficiency of this is so limited that the higher fishes living in well-aerated waters, though descendents of ganoids, have turned a primitive breathing organ to other uses and have reverted wholly to the use of gills. The function of the air-bladder was, then, to tide over periods of partial asphyxiation in foul waters, and seems to have been initially developed from a habit of swallowing air, gasping and finding this mode of relief. If forced to rely wholly upon this, it sufficed merely to keep the fishes alive until a new season of floods should recur, expanding the sphere of action and the supply of food simultaneously with the renewed gill-respiration and increased activity of the inhabitants of the river and playa waters. The use of gills, furthermore, could not become completely eliminated until such great changes had progressed in the heart and circulation inherited from elasmobranchs as are found in modern lung fishes and amphibians. It was this initial inefficiency of air-breathing which seems the strongest proof that it was an adaptation forced by the compulsion of nature, not the expression of a hypothetical innate tendency for advancement in organization. Of course, the organisms must possess at the same time an instability of germ plasm, permitting variations or mutations to arise. These would under the law of probabilities be more often degenerative than ascensive, but the strenuous environmental conditions cut off unsparingly all but the favored few which showed increased efficiency in meeting the critical factor in the environment. The rising death rate owing to recurrences of seasons of marked aridity was the ultimate cause back of the rise of air-breathing vertebrates. Natural selection, by the survival of the fittest, is shown thus, by matching the advance in life to the necessities of environment, to be the overarching cause which led the vertebrates to the possession of the land, their future theater of high evolution. It is doubtful in view of this conclusion if vertebrates could have attained their present dominance of the land without the driving effect of climatic adversities such as are found in the Devonian.

The biologist who studies variations, mutations, Mendelian factors, hybridization; the paleontologist who studies orthogenetic variations, the budding and expansion of phyla, are looking at the expressions of internal forces. These, however, do not constitute a complete picture of the cause and effects of organic evolution any more than the observer of a running antelope could fully explain its flight as the result of the coördination of nervous and muscular actions on a skeletal framework. He must also take into account the ultimate cause—the carnivore behind, and also the carnivores which pursued its ancestors through millions of years. The ultimate controls of evolutions are found in a study of the geologic record, though the possibilities of evolution must be latent within the organism. Natural selection, although discredited as a cause determining specific variations, appears nevertheless to be a major factor in evolution, the driving cause in association with changes in environment, which has forced the great advances in organic progress.

[1] This paper was given orally by the author before the American Society of Vertebrate Paleontology, December 26, 1907 [Loomis, F. B., *Secretary*, The American Society of Vertebrate Paleontology, *Science*, 27, 254–256 (1908)], and also before the Geological Society of America at Washington, December 28, 1915, and the complete paper will be published in the *Bulletin* of that Society in 1916. Some discussion of the subject has also been given by Professor Schuchert in his recent text on *Historical Geology* (Part II of Pirsson-Schuchert, *Text Book of Geology*.

[2] Chamberlin, T. C., On the Habitat of the Early Vertebrates, *J. Geol.*, 8, 400–412 (1900).

[3] Walcott, C. D., Preliminary Notes on the Discovery of a Vertebrate Fauna in Ordovician Strata, *Bull. Geol. Soc. Amer.*, 3, 153–172 (1892).